esa

ECOSPHERE

Can sugar maple establish into the boreal forest? Insights from seedlings under various canopies in southern Quebec

ALEXANDRE COLLIN,[1] CHRISTIAN MESSIER,[1,2] STEVEN W. KEMBEL,[1,3] AND NICOLAS BÉLANGER[1,4,†]

[1]*Centre d'étude de la forêt, Université du Québec à Montréal, C.P. 8888, Succ. Centre-Ville, Montréal, H3C 3P8 Québec Canada*
[2]*Institut des Sciences de la Forêt Tempérée, Université du Québec en Outaouais, 58 rue Principale, Ripon, J0V 1V0 Québec Canada*
[3]*Département des Sciences Biologiques, Université du Québec à Montréal, C.P. 8888, Succ. Centre-Ville, Montréal, H3C 3P8 Québec Canada*
[4]*UER Science et Technologie, Téluq, Université du Québec, 5800 rue Saint-Denis, Bureau 1105, Montréal, H2S 3L5 Québec Canada*

Citation: Collin, A., C. Messier, S. W. Kembel, and N. Bélanger. 2018. Can sugar maple establish into the boreal forest? Insights from seedlings under various canopies in southern Quebec. Ecosphere 9(1):e02022. 10.1002/ecs2.2022

Abstract. Understanding tree recruitment dynamics in various growth environments is essential for a better assessment of tree species' adaptive capacity to climate change. We investigated the microsite factors influencing survival, growth, and foliar nutrition of natural and planted sugar maple seedlings (*Acer saccharum*) along a gradient of tree species that reflect the change in composition from temperate hardwoods to boreal forests of eastern Canada. We specifically tested whether the increasing abundance of conifers in the forest and its modifications on soil properties negatively affects foliar nutrition of natural seedlings as well as the survival and growth of seedlings planted directly in the natural soil and in pots filled with enriched soil. Results of natural seedlings indicate that under conifer-dominated stands, lower soil pH, accelerated dissolution of some minerals, lower temperature and moisture, and higher levels of phenolic compounds have created microsites that are less suitable for sugar maple foliar nutrition and regeneration. These conditions were omnipresent under hemlock. The growth of seedlings planted in the natural soil was negatively impacted by the overall low soil quality under all forest types (as compared to seedlings planted in pots with enriched soil). However, survival and growth of the seedlings were not negatively affected by conifers, regardless of planting type, likely because of stored nutrients from the nursery. Also, lower survival was found under maple–birch stands for seedlings planted both in the natural soil and in pots with enriched soil due to higher shading. This study has identified key microsite factors created by specific conifers that may impede or benefit the potential of sugar maple to maintain its current range or expand its range northward under climate change.

Key words: *Acer saccharum;* conifers; mineral weathering; phenols; seedlings; soil acidity; soil microclimate; survival.

Received 22 May 2017; revised 2 October 2017; accepted 17 October 2017. Corresponding Editor: Nancy C. Emery.

† **E-mail:** nicolas.belanger@teluq.ca

INTRODUCTION

Temperate tree species at their northern range are faced with a rapidly changing climate that could provide opportunities for expanding their range northward (Parmesan and Yohe 2003, Rosenzweig et al. 2008, St. Clair et al. 2008, Chen et al. 2011). The shifts in tree species distributions are expected to be particularly large for populations at the limits of their distribution ranges (Iverson et al. 2004). The distribution of plant species is mainly determined by climatic factors, soil properties, light availability, and biotic interactions (e.g., browsing, pathogens, invading weeds), which, in combination, constrain the survival and development of the populations (Whittaker 1970, Woodward 1987, Gaston 2009). While many studies observed slower shifts in plant species distribution than climate change itself (Parmesan and Yohe 2003, Loarie et al. 2009, Chen et al. 2011,

Zhu et al. 2012), an increasing number of studies suggest that non-climatic factors such as soil properties and biotic interactions are slowing down the migration ability of plant species (McMahon et al. 2011, Brown and Vellend 2014, Graignic et al. 2014, Collin et al. 2017).

Tree recruitment dynamics within new growth environments, including seed germination and seedling survival and adaptation to growth, are poorly understood. Yet, this seems essential for a better assessment of tree species recruitment and sustainability in environments receiving new species in the context of climate change (Gaston 2009, Cleavitt et al. 2014). Over centuries, resident environments have developed into complex biochemical systems that may not always be welcoming to migrating species in terms of their establishment, survival, nutrition, and growth. Positive feedbacks in plant communities (Wilson and Agnew 1992) imply that certain species have created conditions in the resident environment to their benefit and to the disadvantage of migrating plant species. Those conditions can be as varied as acidic soil conditions, low water status, limited soil nutrient and light availability, allelopathic toxin production, and microbe–plant associations that can be harmful to other plants (Binkley and Giardina 1998). For example, in the pygmy forest of northern California, the high levels of polyphenolics in *Pinus muricata* litter control the dominant form in which nitrogen is mobilized, favoring its recovery through pine-mycorrhizal associations and minimizing its availability to competitors (Northup et al. 1995). Some tree species are also more prone to specific fire regimes, which can be a disadvantage for other tree species (Wirth 2005). This was observed in Siberian forests growing on sandy soils with intermediate water and nutrient availability, where the presence of fire-resistant *Pinus sylvestris* favors recurring surface fires that lead to the exclusion of non-resistant *Betula* species (Furyaev et al. 2001). Conversely, some plant species have developed strategies to augment soil nutrient availability and uptake, which likely gives them an advantage over other species. For example, some tree species have the capacity to access deep mineral soil sources to satisfy nutrient demand (Blum et al. 2002, Dijkstra and Smits 2002, Jobbágy and Jackson 2004). An example of this capacity was observed in temperate forests of northeastern America where sugar maple trees (*Acer saccharum* Marsh., hereafter referred to as "maple") maintain a higher density of fine roots deep in the mineral soil (to 60 cm depth) as a means to sustain their high Ca demand (Dijkstra and Smits 2002). In other cases, some tree species may even release large amounts of organic acid exudates from their roots and dissolved CO_2 (to form H_2CO_3), thus promoting soil mineral weathering and the release of Ca, Mg, K, and P from the crystal lattices of minerals. This latter process is influenced by species composition (mostly conifers and late-successional species; Quideau et al. 1996, Augusto et al. 2000), colonization of their roots by mycorrhizal fungi (Hoffland et al. 2004), fast growth (Bélanger et al. 2004), and soil mineralogy (Lafleur et al. 2013).

Interactions and feedback cycles between species and site conditions may explain the actual failure of most models to simulate species migration rates as they are most often only calibrated to regional climates (Clark et al. 2014). Understanding the effects of resident soils (Lafleur et al. 2010) and resident species (Ettinger and HilleRisLambers 2013) thus seems crucial to consider interaction and feedback cycles for the prediction of plant species redistribution under climate change. Maple is of particular interest given the current challenge facing its recruitment and sustainability at both its northern and southern limits in eastern North America. It is proposed that the acidic soil conditions associated with the conifer-dominated boreal forest will limit the northward migration of maple under climate change (Graignic et al. 2014). The growth and survivorship of maple are particularly sensitive to acidic and nutrient-poor soils (St. Clair et al. 2008). Many of the declining maple stands in eastern North America have been related to soil acidification and base cation imbalances caused by acid rain, subsequently leading to foliar Ca and Mg deficiencies and crown decline (Duchesne et al. 2002, Kobe et al. 2002, Juice et al. 2006, Long et al. 2009). Hence, acidic and nutrient-poor soils with thick forest floors (characterized by low N mineralization rates) generally found in the boreal forest of the Precambrian Shield (Moore et al. 1999, Trofymow et al. 2002) may negatively affect early stages of maple seedling establishment, thus limiting its migration potential into the boreal forest. The negative effect of coniferous canopies on foliar nutrient status (mostly Ca and Mg) of maple seedlings was

demonstrated at various latitudes in Quebec (Collin et al. 2017).

The objectives of this study were to test whether the survival, growth, and foliar nutrition of natural and planted maple seedlings are negatively affected by the soil conditions created by coniferous stands. More specifically, we hypothesized that (1) natural maple seedlings under coniferous stands will have decreased foliar nutrition (i.e., N, P, K, Ca, and Mg foliar levels) compared to hardwoods, (2) seedlings planted in the natural soil under coniferous stands will have lower survival and growth rates (mostly due to reduced soil quality) compared to hardwoods, and (3) seedlings planted in pots filled with enriched soil will show similar survival and growth rates between forest types.

Materials and Methods

Study site

The study site is located at the *Station de biologie des Laurentides* (SBL) of the *Université de Montréal* in St. Hippolyte, Quebec (45°59′ N; 74°00′ W), 80 km north of Montreal. Thirty-year average precipitation at SBL is 1100 mm, with 30% falling as snow. Mean annual temperature is 3.6°C. The SBL is found at the transition with the boreal forest, within the northern limit of the maple–yellow birch (*Betula alleghaniensis* Britton) bioclimatic domain of the lower Laurentians (Saucier et al. 2009). Due to its geographic position and history of frequent fires, the area has developed into a mosaic of tree species. Maple is found concomitantly with red maple (*Acer rubrum* L.), yellow birch, poplars (*Populus* spp. L.), balsam fir (*Abies balsamea* (L.) Mill.), white spruce (*Picea glauca* Moench), and northern white cedar (*Thuja occidentalis* L.). It was therefore possible to find a gradient of forest tree species that reflect the change in composition from the southern hardwood to the northern boreal forest of Quebec, which included plots with no maple regeneration under conifer-dominated stands. The soils are Orthic Humo-Ferric Podzols with a sandy loam texture (Soil Classification Working Group 1998). The forest floor is a moder humus form of 5–10 cm. The soils were developed from rocky glacial till derived in part from the underlying anorthosite pluton of the Morin series (Doig 1991), but due to the small size of the pluton, they have a mineral composition that also reflects the mixture of more felsic rocks (e.g., charnockite, mangerite, syenite) in the surroundings of the anorthosite which were mixed by continental ice sheets during the Pleistocene (Bélanger et al. 2012).

Experimental design

Four plots (50 × 50 m) of each of these five forest canopies were delineated: (1) hardwood stands of maple and birch spp., (2) mixed hardwood–conifer stands with a higher dominance of hardwoods, (3) mixed hardwood–conifer stands with a higher dominance of conifers, (4) conifer-dominated stands with maple seedlings, and (5) conifer-dominated stands with at least one maple tree present but with no maple regeneration (5 species composition × 4 repetitions = 20 plots). Basal area of each plot was measured for each tree species present on stems ≥9 cm in diameter at breast height so that the percent contributions of all species to total basal area of the plot could be calculated individually (see Table 1). The percent contributions of hardwoods and conifers to total basal area were also computed individually. Environmental data such as elevation, slope, and exposure were noted to characterize each plot.

Planting experiment (survival and growth)

A planting experiment was conducted in the plots with the specific goal of identifying the factors explaining maple regeneration failure under conifer-dominated stands. Two-year-old bare root maple seedlings (*Ministère des Forêts, de la Faune et des Parcs* tree nursery, Berthier, Quebec, Canada) varying in size from 25 to 45 cm were planted in each plot. Two types of planting were made to isolate the effects of soil chemistry from other effects on seedling survival. First, five seedlings were directly planted in the natural soil using a planting shovel. Second, three seedlings were planted into 4-L pots filled with a mix (1:3 ratio) of local mineral soil and a premium potting mix (PRO-MIX; Rivière-du-Loup, Quebec, Canada) containing peat, perlite, limestone, and the MicoActive organic growth enhancer (i.e., vesicular–arbuscular mycorrhizae). The soil mixture was also fertilized twice during the growing season with a fertilizer for trees (N: 8%, P_2O_5: 2%, K_2O: 2%, Mg: 1.5%, Ca: 8%, S: 5%, Fe: 0.3%; McInnes Natural Fertilizers, Stanstead, Quebec, Canada), thus providing the nutrients required for maple seedling growth. To ensure

Table 1. Total basal area of the various forest types studied and individual contributions by species.

Basal area	SMBi	MH	MC	C	C-nr
Total basal area (m^2/ha)	37 ab	31.5 b	28.25 b	50 a	53.33 a
Individual contribution to basal area by species (%)					
Acer saccharum	69	24.75	3.25	1.75	0
Acer rubrum	0	9.75	15.25	3.5	6.67
Betula papyrifera	2.25	40	25.75	24.75	16.67
Betula alleghaniensis	22.5	0	0	0	0
Fagus grandifolia	4	2.5	1.25	0	0
Populus grandidentata	0	13.5	3.5	0	0
Abies balsamea	2.25	9.5	28	12.5	20.67
Pinus strobus	0	0	14	16.5	0
Picea sp	0	0	3.5	15.25	0
Thuja occidentalis	0	0	5.5	13.25	20.33
Tsuga canadensis	0	0	0	12.5	35.67
Contribution to basal area by general taxa (%)					
Hardwoods	97.75	90.5	49	30	23.34
Conifers	2.25	9.5	51	70	76.67

Notes: Different letters indicate a statistically significant difference for total basal area at $P < 0.05$. Percent contributions by individual species were not tested. SMBi is maple–birch stands, MH is mixed hardwood–conifer stands with dominance of hardwoods, MC is mixed hardwood–conifer stands with dominance of conifers, C is conifer-dominated stands, and nr is no maple regeneration.

that the seedlings in the pots were growing under the same light conditions as the seedlings planted in the natural soil, pots were completely buried in the ground so that all seedlings were growing at the same level. In total, 160 maple seedlings were planted, that is, 100 in natural soil and 60 in pots. All seedlings were marked with numbered flags and were left to grow for two full growing seasons (May 2013 to September 2014). Total height was recorded at planting on all seedlings and at final sampling in September 2014 only on the seedlings that survived. Seedlings were visually inspected five times during the experiment for browsing and leaf pathogens. Survival and total height were also monitored during each of these visits.

Foliage of natural seedlings

In each plot, maple leaves were sampled in early August of 2013 from five naturally growing seedlings (varying in size from 18 to 40 cm) after recording their morphology (i.e., total height and diameter at the ground level). Upon arrival in the laboratory, the leaves were weighed and surface area was measured using the WinFOLIA software (Regent Instruments, Quebec City, Quebec, Canada). WinFOLIA was also used to compute a proxy for herbivory. The software allows calculating the surface of holes that were created by herbivores relative to the total leaf area; that is, the damaged areas were reported as a percentage of the total leaf area. This was further used as a percentage of minimum observed herbivory for comparison between forest types. Leaves were also visually inspected for leaf pathogens before being further processed in the laboratory. Leaf samples were then oven-dried for 72 h at 65°C, weighed, and finely ground using a planetary ball mill (Vibratory Micro Mill Pulverisette 0; Fritsch GmbH, Idar-Oberstein, Germany). Leaf subsamples were then analyzed for C, N, P, K, Ca, and Mg levels (Collin et al. 2017).

Light availability

Three hemispherical photographs were taken in all sample plots and at different places in July 2014 at 1 m aboveground to characterize the light environment in each sampling area. We used a Fujifilm FinePix S 4600 digital camera (Fujifilm Corporation, Tokyo, Japan) that was equipped with a hemispherical Fisheye Converter FC-E8 lens, which was itself mounted on a Fotodiox lens mount adapter (Nikon to Canon EOS). In total, 60 pictures were taken and analyzed with the Gap Light Analyzer (GLA) v2.0 software (Frazer et al. 2000). The GLA software computes the percentage of canopy openness and the effective leaf area index by separating the pixels of the hemispherical pictures into sky and non-sky classes. Based on the canopy openness and environmental data respective to each plot (i.e., geographic location,

elevation, slope, exposure, growing-season length, sky-region brightness, and seasonal patterns of cloudiness), the software further runs a solar radiation model to simulate the total above- and below-canopy solar radiation on a daily basis over the course of the growing season.

Soil properties

Soil volumetric water content (VWC) was monitored in both natural and artificial (pots) soils during the 2013 growing season (i.e., monthly between May and September, five measurements per soil type per plot) at a depth of 7.5 cm using a FieldScout TDR 300 Soil Moisture Meter (Spectrum Technologies Inc., Aurora, Illinois, USA). Soil temperature was recorded for a full year (i.e., May 2013 to May 2014) using temperature data loggers (Thermochron iButtons, model DS1921G; Maxim Integrated Products Inc., Sunnyvale, California, USA). A total of 40 temperature data loggers were distributed among the plots (i.e., one in the soil and one in a pot), buried at a depth of 10 cm, and set to record data every six hours. At the end of one year, loggers were retrieved to extract the data.

Soil samples of forest floor (Oe–Oa) and upper B horizons were also collected during the 2013 growing season at five different locations within each plot. Upon arrival in the laboratory within 12 h, the samples were air-dried before sieving with a 2-mm mesh to remove any coarse fragments. Ground subsamples of both horizons were then analyzed for pH and organic C and total N levels (Collin et al. 2017). Particle size distribution was also analyzed on B horizon samples (≤2 mm), but due to the high organic matter levels of some samples, subsamples were treated by loss on ignition (850°C) before analysis.

Ion-exchange resin (i.e., Plant Roots Simulator [or PRS] probes [Western Ag Innovations, Saskatoon, Saskatchewan, Canada]) were used to assess the soil solution ionic activity (notably NO_3^--N, NH_4^+-N, $H_2PO_4^-$-P, Ca^{2+}, Mg^{2+}, K^+, Al^{3+}, Fe^{3+}, and Mn^{2+}). Within each plot, three pairs of cation and anion probes were randomly inserted vertically under the Oe–Oa horizons at a depth of 10 cm in early June of 2013. Care was taken to insert the probes with as little disturbance as possible. Probes were finally collected 8 weeks later. The PRS probes is an improved method compared to conventional extractions of soils sampled at a particular point in time as they allow for a dynamic measurement of ions flowing through the soil over time. Results of the PRS probes are highly correlated with conventional methods such as Mehlich III extraction (Collin et al. 2017) and are now being frequently used for forest ecology research (Hangs et al. 2004, Moukoumi et al. 2012, Bilodeau-Gauthier et al. 2013). Handlings of the probes in the laboratory after they were extracted from the field as well as analytical protocols are described in Collin et al. (2017).

Free phenols were monitored by placing three polyester N-free bags (50 μm porosity; ANKOM Technology, Macedon, New York, USA) per plot. The bags were filled with 1 g dry weight of XAD-7 resin (Rohm and Hass, Philadelphia, Pennsylvania, USA) and were placed under the Oe–Oa horizons. They were allowed to remain in the field for a 2-month period (July and August 2013). Upon collection, resin bags were returned to the laboratory where they were frozen at −20°C until analysis. Total phenols in resin bags were analyzed following a sequential extraction with water followed by 50% aqueous methanol (Morse et al. 2000). Each capsule was placed in a polypropylene centrifuge tube with 30 mL of distilled water and shaken for 30 min. The aqueous fraction was later decanted into a glass vial and frozen at −20°C until analysis. The resin was then immersed in 10 mL of 50% aqueous methanol and shaken for 30 min. Extracts were decanted into clean glass vials and the process repeated two additional times to create a total extraction volume of 30 mL. The methanol extracts were stored at −20°C until analysis. Total phenol analysis was performed using the modified Prussian blue technique to give greater color stability (Graham 1992). Total phenol content was measured against appropriate phenolic standards (0.001 mol/L gallic acid) at 700 nm with the Hitachi spectrophotometer.

Indices of soil mineral weathering

The sequential chemical leaching procedure proposed by Lafleur et al. (2013) was performed on podzolic B horizons sampled in each plot (five per plot) as a means to determine the levels of exchangeable (i.e., adsorbed on exchange surfaces) and non-exchangeable (i.e., within the crystal lattice of minerals) base cations. This approach can also be used to selectively dissolve minerals and, in turn, determine assemblages of minerals in the soil when a more complete chemical analysis of

the leaches is performed, for example, total P (Bélanger et al. 2012). Specifically, organic matter was first removed from the soil by loss on ignition. Three grams of that soil was thoroughly washed several times with nanopure water to remove the excess ash which can contain high amounts of nutrients, notably base cations. Exchangeable cations adsorbed onto the soil exchange complex were then extracted with 30 mL of 1 mol/L NH_4Cl solution for 2 h on an end-over-end shaker. The intermediate step consisted in a leach performed for 2 h on the end-over-end shaker with 30 mL of 0.1 mol/L HCl. The 0.1 mol/L HCl leach attacks the most easily weathered minerals, thus releasing nutrients from minerals such as free calcite and epidote and some apatite (Drouet et al. 2005, Nezat et al. 2007). The final leach was performed again for 2 h on the same shaker with 1 mol/L HNO_3. The 1 mol/L HNO_3 leach attacks more resistant minerals, thus releasing nutrients from minerals such as apatite, biotite, hornblende, and some K-feldspars (Nezat et al. 2007, Bélanger and Holmden 2010). Each extract/leach was filtered and stored in the fridge until analysis. The extracts and leaches were analyzed for Ca, Mg, and Na concentrations by atomic absorption/emission spectroscopy (model AA-1475, Varian, Palo Alta, California, USA) and P concentration by colorimetry (molybdenum blue) using a Technicon Auto-Analyzer (Technicon Instruments Corporation, Tarrytown, New York, USA). The results were used to assess base cation levels within the crystal lattice of assemblages of minerals (operationally defined as susceptible vs. less susceptible to weathering).

Statistical analyses

Data were analyzed using the statistical software package R version 3.0.0 (R Core Development Team 2013). Descriptive statistics were used to characterize each forest type, to compute correlation and linear regression coefficients of determination between foliar and soil variables, and to compare foliar and soil variables between forest types. Linear mixed-effect models were used in an attempt to consider the blocking structure of the experimental design (with plots being included as random factors) in order to test for the significance of differences of measured variables (foliar, soil, etc.) between forest types (the gradient of the five forest canopies being included as a fixed factor). When testing for the significance of differences of survival and growth for planted seedlings and foliar nutrition of natural seedlings between forest types, original height differences were included as co-variables in the mixed models. This was followed by means separations using Tukey's honest significant difference (HSD) tests. Normality of residuals was verified prior to analysis, and data were transformed when necessary. Analyses were developed using the *lme* function in the *nlme* package (Pinheiro et al. 2014), and Tukey's HSD tests were performed using the *glht* function in the *multcomp* package (Hothorn et al. 2008).

Linear discriminant analysis (LDA) was used to confirm that forest types have different soil properties. For doing so, the multivariate homogeneity of variances within groups was first tested using the *betadisper* function available in the *vegan* library (Oksanen et al. 2013). The LDA was then performed on normalized data with the *lda* function from the *MASS* package and using forest type as a grouping factor. In order to test whether all observations were correctly classified among forest types, a posteriori analysis of correct classification was done using the *predict* function available in the *vegan* library.

Redundancy analysis followed by variation partitioning was used to explain the variation in foliar nutrients by explanatory variables (e.g., soil chemistry and particle size distribution, canopy openness, tree basal area) and quantify their individual contributions to the total explained variation. Analyses were respectively used on normalized data with the *rda* and *varpart* functions, both available in the *vegan* package. Prior to these analyses, testing of multi-collinearity within the matrices (using calculation of variance inflation factors) and a forward selection of explanatory variables had been performed using the *forward.sel* function in the *packfor* package (Dray et al. 2013).

To explore the determinant of survival and growth rates, a regression tree analysis was used with environmental variables as predictors for classifying the presence/absence of seedlings planted in the natural soil at the end of the experiment. This method is more appropriate than linear regressions as it allows to detect for interactions and nonlinearities when numerous predictors are present. Analysis was performed using the *ctree* function of the *party* package (Strobl et al. 2009).

All coefficients of determination (R^2) that were obtained from the aforementioned analyses, and which were reported in this study as a means of explaining variation in the data set, are the adjusted R^2 values, hereafter denoted as R^2_a. The R^2_a is the unbiased form of the coefficient that takes into account the number of input variables in the model. It is required when performing variation partitioning (Peres-Neto et al. 2006). When not provided directly by the analysis or function, R^2_a was calculated with the *RsquareAdj* function in the *vegan* package.

Results

Stand characteristics and soil properties

Basal area of conifer-dominated stands was significantly higher than that of mixed hardwood–conifer stands (Table 1). For variables computed using the GLA software, canopy openness was the only one found to be significantly different between forest types, maple–birch stands having significantly lower canopy openness than mixed hardwood–conifer and conifer-dominated stands without maple seedling regeneration (Table 2). Light availability also tended to be lower under maple–birch stands than under other forest types, but this was not statistically significant.

Linear discriminant analysis showed a clear partitioning of soil properties between hardwood stands, including mixed hardwood–conifer stands dominated by hardwoods, and conifer-dominated stands, including mixed hardwood–conifer stands dominated by conifers (Fig. 1). Both types of mixed hardwood–conifer stands tended, however, to separate from either hardwood- or conifer-dominated stands along the second axis. Also, a posteriori analysis indicated 100% of correct classification for each measurement to the designed class of forest types. The discrimination appears to be mainly driven by soil temperature, VWC, phenols, and soil solution Ca and Mg activities.

Average forest floor pH values ranged from 4.03 to 4.47, with conifer-dominated and mixed hardwood–conifer stands dominated by conifers being the most acidic, followed by mixed hardwood–conifer stands dominated by hardwoods

Table 2. Canopy openness, effective leaf area index (LAI), and light availability in the various forest types studied.

Forest type	Canopy openness (%)	LAI	Light transmitted ($mol \cdot m^{-2} \cdot d^{-1}$)
SMBi	23.76 (±1.74) b	1.93 (±0.11)	10.59 (±0.87)
MH	30.93 (±3.12) a	1.57 (±0.18)	13.99 (±1.96)
MC	30.60 (±1.88) a	1.60 (±0.14)	12.27 (±0.97)
C	28.67 (±1.90) ab	1.65 (±0.11)	11.95 (±0.90)
C-nr	32.90 (±1.45) b	1.53 (±0.06)	13.86 (±0.69)

Notes: Means are presented with standard errors. Different letters indicate a statistically significant difference at $P < 0.05$. The effective LAI was integrated over the zenith angles 0–60° from the hemispherical pictures (see Stenberg et al. 1994). SMBi is maple–birch stands, MH is mixed hardwood–conifer stands with dominance of hardwoods, MC is mixed hardwood–conifer stands with dominance of conifers, C is conifer-dominated stands, and nr is no maple regeneration.

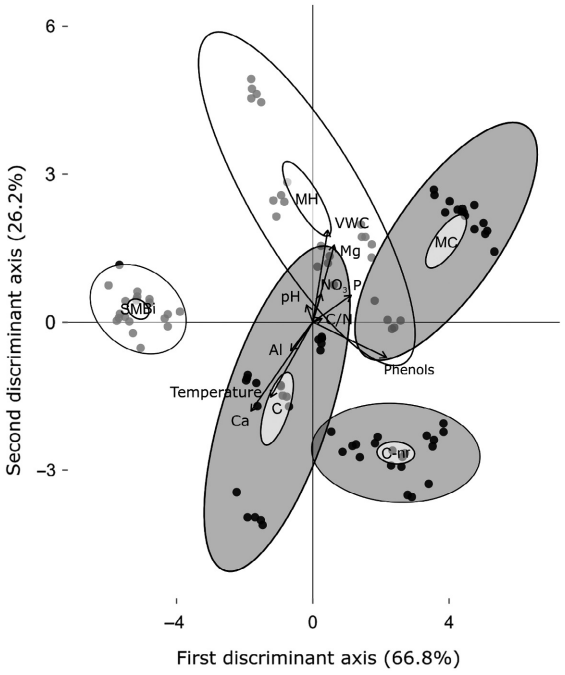

Fig. 1. Linear discriminant analysis of soil chemical properties (i.e., pH, soil solution ionic activity, and phenolic compounds), temperature, and volumetric water content (VWC) by forest type. Gray ellipses indicate conifer-dominated stands. The ellipses surround 95% of the theoretical inner-group dispersion. A posteriori analysis indicated 100% of correct classification for each measurement to the designed class of forest types. SMBi is maple–birch stands, MH is mixed hardwood–conifer stands with dominance of hardwoods, MC is mixed hardwood–conifer stands with dominance of conifers, C is conifer-dominated stands, and nr is no maple regeneration.

Table 3. Physical and chemical properties of the forest floors and upper B horizons in the various forest types studied.

Forest type	pH	VWC (%)	Temperature (°C)	Clay (%)	Silt (%)	Sand (%)
Oe–Oa horizons						
SMBi	4.47 (±0.10) ab	20.32 (±1.20) a	7.15 (±0.12) ab			
MH	4.26 (±0.09) abc	16.18 (±1.30) ab	7.14 (±0.10) ab			
MC	4.12 (±0.08) c	12.30 (±1.10) bc	6.66 (±0.16) abc			
C	4.03 (±0.07) c	13.80 (±0.39) bc	6.69 (±0.12) bc			
C-nr	4.11 (±0.12) bc	11.03 (±0.58) c	6.63 (±0.06) c			
Upper B horizon						
SMBi	4.98 (±0.10) a			2.20 (±0.41)	38.44 (±1.60)	59.37 (±1.96)
MH	5.05 (±0.08) a			2.93 (±0.34)	41.06 (±2.21)	56.01 (±2.51)
MC	5.16 (±0.12) a			2.80 (±0.35)	33.55 (±3.41)	63.66 (±3.75)
C	4.90 (±0.17) a			2.21 (±0.44)	35.37 (±1.67)	62.43 (±2.07)
C-nr	4.55 (±0.20) b			3.92 (±0.14)	48.16 (±2.49)	47.91 (±2.55)

Notes: VWC is volumetric water content. Means are presented with standard errors. Different letters indicate a statistically significant difference at $P < 0.05$. SMBi is maple–birch stands, MH is mixed hardwood–conifer stands with dominance of hardwoods, MC is mixed hardwood–conifer stands with dominance of conifers, C is conifer-dominated stands, and nr is no maple regeneration.

and maple–birch stands (Table 3). pH values in the B horizons ranged from 4.55 to 5.16 and the trend in acidity with conifers was not as apparent, although conifer-dominated stands without maple seedling regeneration were significantly more acidic than all other forest types. Top soil VWC and temperature significantly decreased from hardwoods to conifer-dominated stands (Table 3). Particle size distributions of the B horizons were quite homogeneous across forest types (Table 3). They were characterized by low clay contents (2.20–3.92%), with silt and sand averaging 40% and 57%, respectively. Conifer-dominated stands with no maple seedling regeneration had slightly higher silt and clay and lower sand contents than other forest types.

Soil solution ionic activities differed substantially between forest types (Table 4) and were related to forest floor VWC ($R^2_a = 0.32$, $P < 0.001$, $n = 100$, multivariate relationship) and pH ($R^2_a = 0.26$, $P < 0.001$, $n = 100$, multivariate relationship). Soil solution NO_3^- and NH_4^+ (hereafter referred to as N), Ca, Mg, and Al activities were higher in maple–birch stands than in mixed hardwood–conifer and conifer-dominated stands.

Soils of conifer-dominated stands without maple seedling regeneration had significantly higher levels of phenols compared to other hardwood-dominated stands (Fig. 2). Conifer-dominated stands with maple seedling regeneration, including mixed hardwood–conifer stands dominated by conifers, showed intermediate levels of phenols in the soil and were significantly higher than maple–birch stands.

Calcium and P levels in the 0.1 mol/L HCl leachates (B horizons) showed a general decrease

Table 4. Soil solution ionic activities in the various forest types studied as recorded by the plant roots simulator probes.

Forest type	Soil solution ionic activities (μg·10 cm^{-1}·2 $month^{-1}$)							
	N†	P	K	Ca	Mg	Al	Mn	Fe
SMBi	58.7 (±35.8) a	1.85 (±0.70)	72.7 (±11.3)	787 (±38.4) a	147 (±9.01) a	97.3 (±27.6) a	13.1 (±4.75)	7.07 (±1.47) a
MH	6.00 (±1.04) b	1.93 (±0.69)	72.0 (±7.83)	591 (±100) b	115 (±20.6) ab	38.7 (±3.73) b	5.83 (±1.51)	6.55 (±0.93) a
MC	3.50 (±0.43) b	1.15 (±0.30)	84.0 (±7.41)	389 (±22.7) d	84.0 (±17.2) b	31.5 (±4.21) b	7.13 (±2.38)	5.13 (±1.09) ab
C	3.67 (±0.40) b	3.77 (±2.25)	63.7 (±15.9)	720 (±100) ab	121 (±16.0) ab	39.2 (±4.83) b	8.27 (±1.60)	6.52 (±1.36) a
C-nr	4.00 (±0.51) b	1.78 (±0.29)	72.0 (±0.29)	569 (±62.3) bc	104 (±18.5) b	36.5 (±3.68) b	11.3 (±5.33)	3.15 (±0.50) b

Notes: Means are presented with standard errors. Different letters indicate a statistically significant difference at $P < 0.05$. SMBi is maple–birch stands, MH is mixed hardwood–conifer stands with dominance of hardwoods, MC is mixed hardwood–conifer stands with dominance of conifers, C is conifer-dominated stands, and nr is no maple regeneration.

† Including NO_3^- and NH_4^+.

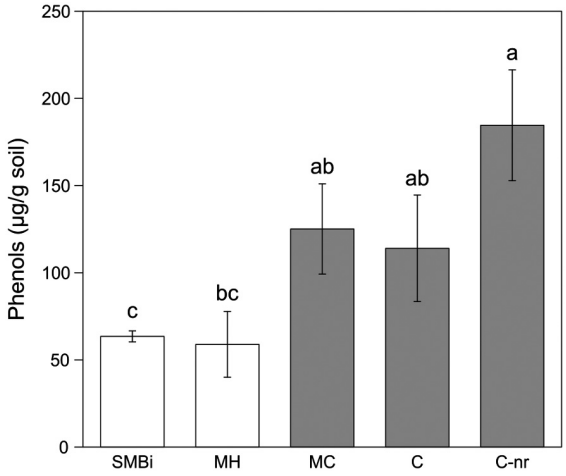

Fig. 2. Levels of phenolic compounds measured under the forest floor of the various forest types studied as recorded by the resin bags. Gray bars indicate conifer-dominated stands. Means are presented with standard errors. Different letters indicate a statistically significant difference at $P < 0.05$. SMBi is maple–birch stands, MH is mixed hardwood–conifer stands with dominance of hardwoods, MC is mixed hardwood–conifer stands with dominance of conifers, C is conifer-dominated stands, and nr is no maple regeneration.

with decreasing forest floor pH and increasing proportion of conifers in the following order: maple–birch stands ≥ mixed hardwood–conifer stands ≥ conifer-dominated stands (Fig. 3A, B). Significantly higher Ca and P levels were found in the higher pH soils of maple–birch stands compared to the more acidic soils of conifer-dominated stands, including mixed hardwood–conifer stands dominated by conifers in the case of P. The mean molar Ca/P ratios in the various forest types were above 4 (Fig. 3C). The mean ratios were similar between most forest types (4–7), except for mixed hardwood–conifer stands dominated by conifers which had a mean molar Ca/P ratio of 11 but a large standard error (Fig. 3C).

Survival and growth (planted seedlings)

After 456 d, 101 out of 160 planted seedlings had survived (63%). Maple seedlings that were planted in pots with enriched soil had a significantly lower survival under maple–birch stands than those under both types of mixed hardwood–conifer stands (Table 5). Comparisons in height growth indicate that maple seedlings planted in pots with enriched soil grew at a significantly higher rate than seedlings planted in the natural soil. However, no significant difference was found in height growth between forest types, whether they were planted in the natural soil or in the pots with enriched soil (Table 5). No pathogen was visually detected on the leaves of any of the seedlings. Results of the regression tree analysis suggested that survival was first best partitioned into two groups using soil solution N activity (threshold at 6 µg N per 10 cm, $P < 0.05$; Appendix S1: Fig. S1). Survival in the first group (under 6 µg N per 10 cm) was further separated by tree basal area, leading to higher probability of mortality above 40 m^2/ha ($P < 0.01$). This corresponds to conifer-dominated stands. Survival in the second group (above 6 µg N per 10 cm) was further separated by soil temperature during the growing season, leading to higher probability of mortality above 7.14°C ($P < 0.01$). This corresponds to maple–birch stands.

Foliar nutrients and herbivory (natural seedlings)

Foliar nutrient levels of naturally regenerated maple seedlings varied significantly between forest types (Table 6). Seedlings under hardwood and mixed hardwood–conifer stands dominated by conifers had higher foliar Ca and Mg levels than under conifer-dominated stands. Foliar N levels were significantly higher in mixed hardwood–conifer stands dominated by conifers than in those dominated by hardwoods. Similarly, seedlings under mixed hardwood–conifer stands dominated by conifers had significantly higher foliar P levels than in any other forest type studied. Leaf scans used in an attempt to characterize the intensity of herbivory did not return significant leaf damage differences on maple seedlings between forest types, nor were any pathogens visually detected on the leaves.

Using redundancy analysis, and after removing collinearities between variables, it was found that the most robust model explaining variation in foliar nutrients was composed of forest floor pH and VWC. This model explained as much as 52% of the variation in foliar nutrients of maple seedlings ($P < 0.001$, $n = 100$). This is a more robust model than expected considering that

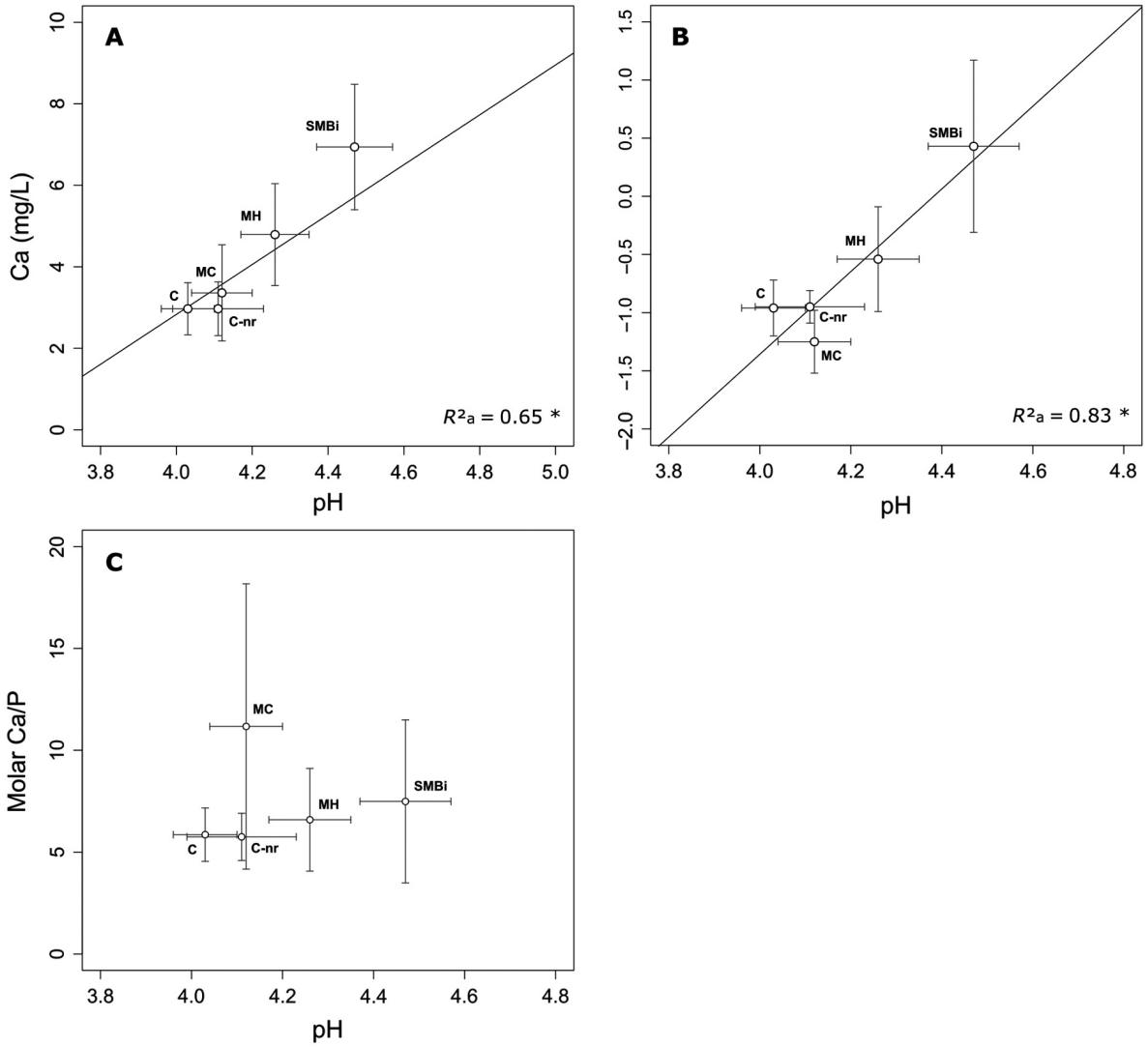

Fig. 3. Relationships between pH and (A) Ca levels, (B) P levels, and (C) molar Ca/P ratios in the 0.1 mol/L HCl B horizon leachates of the various forest types studied. Means are presented with standard errors. SMBi is maple–birch stands, MH is mixed hardwood–conifer stands with dominance of hardwoods, MC is mixed hardwood–conifer stands with dominance of conifers, C is conifer-dominated stands, and nr is no maple regeneration. Statistical significance is designated as *($P < 0.05$).

maple seedlings originated from a natural system with uncontrolled growing conditions, hence increasing variability and uncertainty toward explaining factors. Variation partitioning was also conducted to quantify the respective contribution of each environmental variables selected in the model. Forest floor pH explained 39% of the total variation in foliar nutrients, and soil VWC explained 13% of the total variation.

Discussion

Survival and growth of planted seedlings

On the one hand, the results of the survival experiment did not support our hypothesis that maple seedlings planted in the natural soil are negatively impacted by lower soil quality under conifer stands, nor that seedlings planted in pots with enriched soil would have similar survival

Table 5. Survival rates and relative height growth of the sugar maple seedlings planted in the natural soil and pots with enriched soil under the various forest types studied as measured at the end of the trial (456 d).

Forest type	*n*		Survival rate (%)		Height growth (%)	
	Soil	Pot	Soil	Pot	Soil	Pot
SMBi	7	3	35 (±10.9) ab	25 (±13.1) b	19.9 (±2.4)	36.8 (±17.5)
MH	20	8	100 a	66.7 (±14.2) a	22.5 (±3.4)	44.5 (±12.2)
MC	20	11	100 a	91.7 (±8.3) a	20.4 (±2.5)	47.2 (±12.6)
C	11	7	55 (±11.4) ab	58.3 (±14.9) ab	20.7 (±2.2)	37.1 (±8.9)
C-nr	9	5	45 (±13.3) ab	41.7 (±17.6) ab	23.7 (±4.0)	44.7 (±13.7)
Planting comparison						
P-value			0.371		<0.001	

Notes: Means are presented with standard errors when available. Different letters indicate a statistically significant difference at $P < 0.05$. Relative height growth is given as a percentage (%) of pre-planting height. SMBi is maple–birch stands, MH is mixed hardwood–conifer stands with dominance of hardwoods, MC is mixed hardwood–conifer stands with dominance of conifers, C is conifer-dominated stands, and nr is no maple regeneration.

rates between forest types (Table 5). In fact, lower survival was found for seedlings planted in both the natural soil and pots with enriched soil under maple–birch stands. The result of the regression tree analysis suggesting that a combination of higher soil solution N activity and soil temperature leads to a higher mortality in maple–birch stands is odd (Appendix S1: Fig. S1) and rather suggests that other environmental co-variables are likely responsible for the observed mortality. Preferential insect browsing, herbivory, or leaf pathogens are also not likely explaining survival differences as we observed no difference in these variables between forest types. Instead, the light environment is one factor that better explains the lower survival, as light availability tended to be lower under maple–birch stands compared to the other forest types, but the lower number of replications for this specific variable (i.e., three measurements per plot instead of five for other variables) likely prevented the detection of a significant difference (Table 2). Similarly, the growth rates of seedlings planted under maple–birch stands (both planting conditions) tended to be lower than under any other forest types, despite having the better soil conditions (less acidic soils and better availability of nutrients in the soil solution; Tables 3, 4), hence placing more emphasis on the impact of light availability on seedling performance under maple–birch stands. In addition, seedlings were grown in nursery for 2 yr under optimal nutrient availability prior to being planted. Over 1.5 yr of experimenting, it is possible that nutrient reserves were sufficient for the survival rates of seedlings planted in the natural soil, under lower soil quality, to be similar to those planted in pots with enriched soil (Oliet et al. 2013). The outcome could have been different if seedlings originating from seeds with a local chemical signature were tested. On the other hand, higher height growth of maple seedlings planted in pots with enriched soil compared to those planted in the natural soil (Table 5) confirms that mixing the local mineral soil with a premium potting mix containing peat, perlite, limestone, and vesicular–arbuscular mycorrhizae

Table 6. Foliar nutrient levels of sugar maple seedlings in the various forest types studied.

Forest type	Foliar nutrients (mg/g)					
	C	N	P	K	Ca	Mg
SMBi	468 (±4.58)	18.54 (±1.20) ab	1.14 (±0.08) b	5.87 (±0.66)	8.89 (±0.46) a	2.05 (±0.26) a
MH	467 (±3.35)	17.00 (±0.91) b	1.08 (±0.05) b	6.55 (±0.67)	8.44 (±0.72) ab	1.86 (±0.20) ab
MC	466 (±5.59)	19.03 (±1.28) a	1.29 (±0.08) a	6.62 (±1.11)	9.11 (±0.79) a	2.08 (±0.24) a
C	470 (±5.06)	18.96 (±1.43) ab	1.09 (±0.07) b	6.45 (±0.65)	7.86 (±0.75) b	1.67 (±0.21) b

Notes: Means are presented with standard errors. Different letters indicate a statistically significant difference at $P < 0.05$. SMBi is maple–birch stands, MH is mixed hardwood–conifer stands with dominance of hardwoods, MC is mixed hardwood–conifer stands with dominance of conifers, and C is conifer-dominated stands.

in combination with fertilization provided nutrients for a more optimal growth than the natural soil under all forest types, indicating that the soil, along with light availability, is also a factor limiting growth at the site. Base cation fertilization in St. Hippolyte was shown to improve foliar Ca, Mg, and K nutrition of maple in the short term (Fyles et al. 1994). Many other studies have shown that various forms of fertilization, for example, liming, generally enhance maple health in acidified ecosystems (Moore and Ouimet 2006, Schaberg et al. 2006, Moore et al. 2014).

Regeneration and foliar nutrition of natural seedlings

Foliar chemical analysis of natural maple seedlings supported our hypothesis that these seedlings have decreased foliar nutrition under coniferous stands compared to hardwoods (notably Ca and Mg levels; Table 6). In addition, and contrary to planted seedlings, soil physicochemical analysis and foliar nutrient levels of natural maple seedlings supported that the absence of regeneration under some conifer-dominated stands is related to specific soil physicochemical properties (e.g., pH, water content, temperature; Table 3) and low soil nutrient availability (Table 4) that impede maple regeneration and early seedling growth. Three explanations are provided here. First, conifer-dominated stands with no maple regeneration were found to be dominated by eastern hemlock compared to other conifer-dominated stands (Table 1). Eastern hemlock is a species known to exclude maple by adversely influencing maple germination and seedling regeneration due to unsuitable forest floor conditions (Frelich et al. 1993). The presence of hemlock in some stands in St. Hippolyte may have favored the creation of specific conditions in the forest floor that are not optimal for regeneration success of maple. The thick, acidic, and drier forest floor under the conifer-dominated stands also showed lower soil nutrient availability (including N, Ca, and Mg) than forest floors produced by other forest types (Tables 3, 4). Immobilization of nutrients is typical of recalcitrant forest floors produced mainly from coniferous litters (Augusto et al. 2000). In St. Hippolyte, this led mainly to lower foliar Ca and Mg levels of maple seedlings, suggesting that fitness has been negatively impacted by conifer dominance (Table 6). Maple is known to be very sensitive to Ca and Mg availability for its survival and growth (Houle et al. 2007, St. Clair et al. 2008, Long et al. 2009). Declining maple stands were generally related to low foliar Ca, Mg, and K levels (Côté and Camire 1995, Ouimet et al. 2006, Duchesne and Ouimet 2009), and thus, as indicated above, maple health is generally improved by liming. In St. Hippolyte, Collin et al. (2016) showed a similar foliar imbalance caused by a decrease in foliar Ca and Mg levels with the increasing presence of conifers and soil acidity. Also, while pH of the mineral soil was relatively similar between forest types, conifer-dominated stands without maple regeneration distinguished themselves by having a significantly more acidic mineral soil (Table 3).

Second, soils under conifer-dominated stands without maple regeneration had higher levels of phenolic compounds (Fig. 2). The higher levels of phenols appear to be more easily detected in poor soils where slow organic matter decomposition is accompanied by the characteristic production of phenolic compounds which can inhibit nitrification and thus effectively decrease nutrient availability (Hättenschwiler and Vitousek 2000, DeLuca et al. 2002). Hence, greater soil acidity budgets in forests are likely associated with a greater production of phenols (Blum 2006). Also, it was demonstrated that high levels of phenols can effectively repress maple seed germination and seedling development (Hane et al. 2003). A similar process under conifer stands may be exacerbating maple regeneration in St. Hippolyte. However, because the direct effects of phenols on maple survival were not isolated in our experiment, great care needs to be taken to infer causation.

Third, the absence of maple regeneration under some conifer-dominated stands could be explained by additional factors related to soil microclimate and tree density. To germinate, maple seeds require moist stratification at temperatures slightly above freezing and below 10°C for 35–90 d (Yawney and Carl 1968, Godman et al. 1990). Therefore, lower mean annual soil temperature and VWC during the growing season under conifer-dominated stands (Table 2) is not uncommon (e.g., greater interception of light [Penn et al. 2012] and of rainfall [Carleton and Kavanagh 1990, Lovett et al. 1996, Barbier et al. 2009] by the persistent and dense conifer canopies). This has the potential to further

(negatively) affect maple seed germination and seedling survival at early stages of growth. Seedlings are likely more sensitive to temperature and drought than adult plants because they have smaller and shallower root systems that cannot as easily avoid high soil surface temperatures during hot summer days and water stress by accessing deeper soil water reserves (Niinemets 2010, Fisichelli et al. 2014). Maple seedlings are particularly susceptible to water stress (Hett 1971, Godman et al. 1990). Moreover, conifer-dominated stands have higher basal area (Table 1). This may reflect a higher competition for soil resources. However, we can also consider that for those stands, only very few maple trees were present in the surroundings, thus highly reducing seed availability for colonization.

Differences in soil mineral weathering

Considering the relatively homogeneous parent material in St. Hippolyte in terms of bulk chemical composition and mineralogy at the time it was deposited by the continental ice sheets (Bélanger et al. 2002, 2012) and similar soil textures (Table 3), the results from the sequential leaching of the B horizon samples suggest that the most easily weathered minerals have been leached from the soil at a faster rate under stands with the presence of conifers, that is, mixed hardwood–conifer and conifer-dominated stands, compared to hardwood-dominated stands. This is indicated by lower levels of structural Ca and P in minerals as simulated by HCl leaches of mixed hardwood–conifer and conifer-dominated stands mineral soils, which is related to greater forest floor acidity (Fig. 3A, B). Considering previous work on soil mineralogy in St. Hippolyte (Bélanger et al. 2012), the results can be interpreted by a lower abundance of calcite, apatite, and epidote in the soils of the mixed hardwood–conifer and conifer-dominated stands because of the acidity that they have produced from their litters and other sources (Finzi et al. 1998, Augusto et al. 2000), thus augmenting dissolution rates. Weathering rates were suggested to increase under conifer species such as pines, spruces, and firs because of their capacity to acidify soils (see review by Augusto et al. [2000]). In the long term, higher dissolution rates of easily weathered minerals and greater depletion of soil non-exchangeable base cation reserves under conifer-dominated stands in St. Hippolyte appear to have led to lower foliar Ca and Mg levels of maple seedlings (Table 6). The lower Ca and Mg levels seem to apply to the overall system of conifer-dominated stands as soil solution Ca and Mg activities are also low under this forest type (Table 4).

Mixed hardwood–conifer stands dominated by conifers generally showed the highest foliar P levels among the forest types studied (Table 6). This result was surprising, given that soil solution activities of most nutrient ions tended to be among the lowest of all the forest types studied (Table 4). The fact that molar Ca/P ratios of the HCl leaches under all forest types were above 4 (Fig. 3C) suggests that Ca-rich minerals such as epidote and perhaps calcite (aluminum–iron sorosilicate and calcium carbonate minerals, respectively) are contributing more Ca and less P compared to apatite (pure apatite [$CaPO_4$] has a stoichiometry fixed at a molar Ca/P ratio of 1.66) into the leachates (Bélanger et al. 2012). The Ca/P ratios of the HCl leaches are also generally similar between forest types, which suggest that the minerals have been congruently leached, despite variations in conifer abundance (Fig. 3C). Hence, weathering appears to have occurred at a faster rate where conifers were present, but they did not trigger a preferential dissolution of these easily weathered minerals.

The mixed hardwood–conifer stands dominated by conifers, however, may be one exception to that rule. The higher molar Ca/P ratios of the HCl leaches under this forest type (mean of 11 with a large standard error) could indicate a greater depletion of apatite over epidote and calcite in the long term. Using Sr isotope ratios, balsam fir and red spruce are the ectomycorrhizal tree species that were shown to largely utilize apatite-derived Ca (Blum et al. 2002). It was suggested that ectomycorrhizal fungi produce low molecular weight organic acids that dissolve apatite. In turn, associated roots directly absorb the ions from the crystal lattice of the mineral, thus bypassing the soil solution and exchangeable soil pool. Similarly, bacteria isolated from ectomycorrhizal mycelium of white spruce were recently shown to play an important role on P nutrition by efficiently dissolving apatite (Fontaine et al. 2016). Finally, *Pinus* spp. are also known to have ectomycorrhizal associations with roots that accelerate weathering of minerals and podzolic soil

formation (Van Breemen et al. 2000, Hoffland et al. 2004). On the one hand, the conifers in the mixed hardwood–conifer stands dominated by conifers are mostly ectomycorrhizal species, that is, balsam fir, spruces, and eastern white pine (Table 1; Frank 1990, Wendel and Smith 1990). On the other hand, the conifer-dominated stands have a large proportion of white cedar and eastern hemlock. White cedar is an arbuscular mycorrhizal species, whereas eastern hemlock is both an arbuscular and ectomycorrhizal species (Godman and Lancaster 1990, Johnston 1990). While recent evidence suggests that arbuscular mycorrhizal fungi can also dissolve minerals (Arocena et al. 2012, Koele et al. 2014), they facilitate slower weathering rates than ectomycorrhizal fungi (Quirk et al. 2012). It is therefore possible that the ectomycorrhizal associations with conifer roots under mixed hardwood–conifer stands dominated by conifers degrade the most easily weathered minerals, notably apatite, at a faster rate and to specific levels that favor P nutrition of maple seedlings and perhaps Ca and Mg nutrition as well (as shown by relatively high foliar levels compared to other forest types; Table 6). Since there was low activity of most nutrient ions in the soil solution under hardwood–conifer stands dominated by conifers, including PO_4, Ca, and Mg, we speculate that arbuscular mycorrhizal fungi and perhaps other soil organisms, for example, saprotrophic fungi and rhizosphere bacteria (Clark and Zeto 2000, Koele et al. 2014), have direct access to P, Ca, and Mg ions from the degraded minerals, thus helping to satisfy at least part of the nutritional needs of maple seedlings under that forest type. Candidate minerals other than apatite (P, Ca) for such a mechanism of direct maple seedling nutrition in St. Hippolyte are epidote (Ca) and hornblende (Mg) (Bélanger et al. 2012). As a whole, the conifer tree species that co-exist with maple may therefore be important for determining survival and fitness of maple seedlings establishing in the boreal forest under climate change.

Conclusion

Results from this study indicate that foliar nutrition and regeneration of maple seedlings are strongly influenced by tree species composition. The results support the idea that coniferous species have a negative effect on foliar nutrition of maple seedlings. This effect is governed by the recalcitrant (thick), acidic, and drier forest floor under conifer-dominated stands with low nutrient availability, which leads to poor foliar Ca and Mg nutrition. Calcium and Mg are important for the health and vigor of maples in eastern North America. Although soil quality was lower in conifer stands compared to hardwoods, the survival and growth of the seedlings planted in the natural soil did not differ between forest types. This could be the consequence of a nutrient buildup in the development of the seedlings at the nursery. However, the results of foliar nutrition and soil conditions suggest that the absence of regeneration under some conifer-dominated stands in St. Hippolyte could be related to the long-term acidification of the mineral soil, low soil temperature and moisture, and high soil phenol levels. Such conditions are associated with hemlock dominance in the canopy. The data also suggest an accelerated dissolution of easily weathered minerals (i.e., calcite, apatite, and epidote) under these specific conifer-dominated stands. This suggests that depending on soil properties, maple seedling foliar nutrition and regeneration as well as its potential to establish northward in the boreal forest may be dependent on the coniferous tree species present in the resident forest.

Acknowledgments

Financial support was provided through NSERC (Natural Sciences and Engineering Research Council of Canada) Discovery grants (RGPIN 312369-2010 & 2015-03699) to N.B. We thank Florence Bélanger, Marcelo Frosi, Jacinthe Ricard-Piché, and Fanny Gagné for their help in the field and laboratory. We are also grateful to Marie-Claude Turmel, Hélène Lalande, and Dominic Bélanger for laboratory analyses. Finally, we thank the Station de biologie des Laurentides of Université de Montréal for providing access to the research site.

Literature Cited

Arocena, J., B. Velde, and S. Robertson. 2012. Weathering of biotite in the presence of arbuscular mycorrhizae in selected agricultural crops. Applied Clay Science 64:12–17.

Augusto, L., M.-P. Turpault, and J. Ranger. 2000. Impact of forest tree species on feldspar weathering rates. Geoderma 96:215–237.

Barbier, S., P. Balandier, and F. Gosselin. 2009. Influence of several tree traits on rainfall partitioning in temperate and boreal forests: a review. Annals of Forest Science 66:1–11.

Bélanger, N., B. Côté, F. Courchesne, J. W. Fyles, P. Warfvinge, and W. H. Hendershot. 2002. Simulation of soil chemistry and nutrient availability in a forested ecosystem of southern Quebec—I. Reconstruction of the time-series files of nutrient cycling using the MAKEDEP model. Environmental Modelling & Software 17:427–445.

Bélanger, N., and C. Holmden. 2010. Influence of landscape on the apportionment of Ca nutrition in a Boreal Shield forest of Saskatchewan (Canada) using $^{87}Sr/^{86}Sr$ as a tracer. Canadian Journal of Soil Science 90:267–288.

Bélanger, N., C. Holmden, F. Courchesne, B. Côté, and W. H. Hendershot. 2012. Constraining soil mineral weathering $^{87}Sr/^{86}Sr$ for calcium apportionment studies of a deciduous forest growing on soils developed from granitoid igneous rocks. Geoderma 185–186:84–96.

Bélanger, N., D. Paré, M. Bouchard, and G. Daoust. 2004. Is the use of trees with superior growth a threat to soil nutrient availability? A case study with Norway spruce. Canadian Journal of Forest Research 34:560–572.

Bilodeau-Gauthier, S., D. Paré, C. Messier, and N. Bélanger. 2013. Root production of hybrid poplars and nitrogen mineralization improve following mounding of boreal Podzols. Canadian Journal of Forest Research 43:1092–1103.

Binkley, D., and C. Giardina. 1998. Why do tree species affect soils? The warp and woof of tree-soil interactions. Biogeochemistry 42:89–106.

Blum, U. 2006. Allelopathy: a soil system perspective. Pages 299–340 *in* M. Reigosa, N. Pedrol, and L. González, editors. Allelopathy. Springer, Dordrecht, The Netherlands.

Blum, J. D., A. Klaue, C. A. Nezat, C. T. Driscoll, C. E. Johnson, T. G. Siccama, C. Eagar, T. J. Fahey, and G. E. Likens. 2002. Mycorrhizal weathering of apatite as an important calcium source in base-poor forest ecosystems. Nature 417:729–731.

Brown, C. D., and M. Vellend. 2014. Non-climatic constraints on upper elevational plant range expansion under climate change. Proceedings of the Royal Society Series B 281:20141779.

Carleton, T., and T. Kavanagh. 1990. Influence of stand age and spatial location on throughfall chemistry beneath black spruce. Canadian Journal of Forest Research 20:1917–1925.

Chen, I.-C., J. K. Hill, R. Ohlemüller, D. B. Roy, and C. D. Thomas. 2011. Rapid range shifts of species associated with high levels of climate warming. Science 333:1024–1026.

Clark, J. S., D. M. Bell, M. C. Kwit, and K. Zhu. 2014. Competition-interaction landscapes for the joint response of forests to climate change. Global Change Biology 20:1979–1991.

Clark, R., and S. Zeto. 2000. Mineral acquisition by arbuscular mycorrhizal plants. Journal of Plant Nutrition 23:867–902.

Cleavitt, N. L., J. J. Battles, T. J. Fahey, and J. D. Blum. 2014. Determinants of survival over 7 years for a natural cohort of sugar maple seedlings in a northern hardwood forest. Canadian Journal of Forest Research 44:1112–1121.

Collin, A., C. Messier, and N. Bélanger. 2017. Conifer presence may negatively affect sugar maple's ability to migrate into the boreal forest through reduced foliar nutritional status. Ecosystems 20:701–716.

Collin, A., C. Messier, B. Côté, M. Fontana, and N. Bélanger. 2016. Contrasting nutritional acclimation of sugar maple (*Acer saccharum* Marsh.) and red maple (*Acer rubrum* L.) to increasing conifers and soil acidity as demonstrated by foliar nutrient balances. Frontiers in Ecology and Evolution 4. https://doi.org/10.3389/fevo.2016.00085

Côté, B., and C. Camire. 1995. Application of leaf, soil, and tree-ring chemistry to determine the nutritional-status of sugar maple on sites of different levels of decline. Water, Air, and Soil Pollution 83:363–373.

DeLuca, T., M.-C. Nilsson, and O. Zackrisson. 2002. Nitrogen mineralization and phenol accumulation along a fire chronosequence in northern Sweden. Oecologia 133:206–214.

Dijkstra, F. A., and M. M. Smits. 2002. Tree species effects on calcium cycling: the role of calcium uptake in deep soils. Ecosystems 5:385–398.

Doig, R. 1991. U-Pb zircon dates of Morin anorthosite suite rocks, Grenville Province, Quebec. Journal of Geology 99:729–738.

Dray, S., R. Bivand, P. Legendre, J. Oksanen, F. Blanchet, and P. Solymos. 2013. packfor: forward Selection with Permutation (Canoco p. 46) v. 0.8. https://rdrr.io/rforge/packfor/

Drouet, T., J. Herbauts, W. Gruber, and D. Demaiffe. 2005. Strontium isotope composition as a tracer of calcium sources in two forest ecosystems in Belgium. Geoderma 126:203–223.

Duchesne, L., and R. Ouimet. 2009. Present-day expansion of American beech in northeastern hardwood forests: Does soil base status matter? Canadian Journal of Forest Research 39:2273–2282.

Duchesne, L., R. Ouimet, and D. Houle. 2002. Basal area growth of sugar maple in relation to acid

deposition, stand health, and soil nutrients. Journal of Environmental Quality 31:1676–1683.

Ettinger, A. K., and J. HilleRisLambers. 2013. Climate isn't everything: Competitive interactions and variation by life stage will also affect range shifts in a warming world. American Journal of Botany 100:1344–1355.

Finzi, A. C., C. D. Canham, and N. Van Breemen. 1998. Canopy tree-soil interactions within temperate forests: species effects on pH and cations. Ecological Applications 8:447–454.

Fisichelli, N., A. Wright, K. Rice, A. Mau, C. Buschena, and P. B. Reich. 2014. First-year seedlings and climate change: species-specific responses of 15 North American tree species. Oikos 123:1331–1340.

Fontaine, L., N. Thiffault, D. Paré, J.-A. Fortin, and Y. Piché. 2016. Phosphate-solubilizing bacteria isolated from ectomycorrhizal mycelium of *Picea glauca* are highly efficient at fluorapatite weathering. Botany-Botanique 94:1183–1193.

Frank, R. M. 1990. *Abies balsamea* (L.) Mill. Balsam fir. Pages 26–48 *in* R. M. Burns and B. H. Honkala, editors. Silvics of North America: 1. Conifers. Agriculture handbook. USDA Forest Service, Washington, D.C., USA.

Frazer, G. W., C. Canham, and K. Lertzman. 2000. Gap light analyzer, version 2.0. Bulletin of the Ecological Society of America 81:191–197.

Frelich, L. E., R. R. Calcote, M. B. Davis, and J. Pastor. 1993. Patch formation and maintenance in an old-growth hemlock-hardwood forest. Ecology 74: 513–527.

Furyaev, V. V., E. A. Vaganov, N. M. Tchebakova, and E. N. Valendik. 2001. Effects of fire and climate on successions and structural changes in the Siberian boreal forest. Eurasian Journal of Forest Research 2:1–15.

Fyles, J., B. Côté, F. Courchesne, W. Hendershot, and S. Savoie. 1994. Effects of base cation fertilization on soil and foliage nutrient concentrations, and litter-fall and throughfall nutrient fluxes in a sugar maple forest. Canadian Journal of Forest Research 24:542–549.

Gaston, K. J. 2009. Geographic range limits: achieving synthesis. Proceedings of the Royal Society of London B: Biological Sciences 276:1395–1406.

Godman, R. M., and K. Lancaster. 1990. *Tsuga canadensis* (L.) Carr. Eastern hemlock. Pages 604–612 *in* R. M. Burns and B. H. Honkala, editors. Silvics of North America: 1. Conifers. Agriculture handbook. USDA Forest Service, Washington, D.C., USA.

Godman, R. M., H. W. Yawney, and C. H. Tubbs. 1990. *Acer saccharum* Marsh. Sugar maple. Pages 194–216 *in* R. M. Burns and B. H. Honkala, editors. Silvics of North America: 2. Hardwoods. Agriculture handbook. USDA Forest Service, Washington, D.C., USA.

Graham, H. 1992. Modified Prussian blue assay for total phenols. Journal of Agricultural and Food Chemistry 40:801–805.

Graignic, N., F. Tremblay, and Y. Bergeron. 2014. Geographical variation in reproductive capacity of sugar maple (*Acer saccharum* Marshall) northern peripheral populations. Journal of Biogeography 41:145–157.

Hane, E. N., S. P. Hamburg, A. L. Barber, and J. A. Plaut. 2003. Phytotoxicity of American beech leaf leachate to sugar maple seedlings in a greenhouse experiment. Canadian Journal of Forest Research 33:814–821.

Hangs, R. D., K. J. Greer, and C. A. Sulewski. 2004. The effect of interspecific competition on conifer seedling growth and nitrogen availability measured using ion-exchange membranes. Canadian Journal of Forest Research 34:754–761.

Hättenschwiler, S., and P. M. Vitousek. 2000. The role of polyphenols in terrestrial ecosystem nutrient cycling. Trends in Ecology & Evolution 15:238–243.

Hett, J. M. 1971. A dynamic analysis of age in sugar maple seedlings. Ecology 52:1071–1074.

Hoffland, E., T. W. Kuyper, H. Wallander, C. Plassard, A. A. Gorbushina, K. Haselwandter, S. Holmström, R. Landeweert, U. S. Lundström, and A. Rosling. 2004. The role of fungi in weathering. Frontiers in Ecology and the Environment 2:258–264.

Hothorn, T., F. Bretz, P. Westfall, and R. Heiberger. 2008. Multcomp: simultaneous inference for general linear hypotheses. R Package Version 1.0-3. https://cran.r-project.org/package=multcomp

Houle, D., S. Tremblay, and R. Ouimet. 2007. Foliar and wood chemistry of sugar maple along a gradient of soil acidity and stand health. Plant and Soil 300:173–183.

Iverson, L. R., M. W. Schwartz, and A. M. Prasad. 2004. How fast and far might tree species migrate in the eastern United States due to climate change? Global Ecology and Biogeography 13:209–219.

Jobbágy, E. G., and R. B. Jackson. 2004. The uplift of soil nutrients by plants: biogeochemical consequences across scales. Ecology 85:2380–2389.

Johnston, W. F. 1990. *Thuja occidentalis* L. Northern white-cedar. Pages 1189–1210 *in* R. M. Burns and B. H. Honkala, editors. Silvics of North America: 1. Conifers. Agriculture handbook. USDA Forest Service, Washington, D.C., USA.

Juice, S. M., T. J. Fahey, T. G. Siccama, C. T. Driscoll, E. G. Denny, C. Eagar, N. L. Cleavitt, R. Minocha, and A. D. Richardson. 2006. Response of sugar maple to calcium addition to northern hardwood forest. Ecology 87:1267–1280.

Kobe, R. K., G. E. Likens, and C. Eagar. 2002. Tree seedling growth and mortality responses to manipulations of calcium and aluminum in a northern hardwood forest. Canadian Journal of Forest Research 32: 954–966.

Koele, N., I. A. Dickie, J. D. Blum, J. D. Gleason, and L. de Graaf. 2014. Ecological significance of mineral weathering in ectomycorrhizal and arbuscular mycorrhizal ecosystems from a field-based comparison. Soil Biology and Biochemistry 69:63–70.

Lafleur, B., D. Pare, Y. Claveau, E. Thiffault, and N. Belanger. 2013. Influence of afforestation on soil: the case of mineral weathering. Geoderma 202:18–29.

Lafleur, B., D. Paré, A. D. Munson, and Y. Bergeron. 2010. Response of northeastern North American forests to climate change: Will soil conditions constrain tree species migration? Environmental Reviews 18:279–289.

Loarie, S. R., P. B. Duffy, H. Hamilton, G. P. Asner, C. B. Field, and D. D. Ackerly. 2009. The velocity of climate change. Nature 462:1052–1055.

Long, R. P., S. B. Horsley, R. A. Hallett, and S. W. Bailey. 2009. Sugar maple growth in relation to nutrition and stress in the northeastern United States. Ecological Applications 19:1454–1466.

Lovett, G. M., S. S. Nolan, C. T. Driscoll, and T. J. Fahey. 1996. Factors regulating throughfall flux in a New Hampshire forested landscape. Canadian Journal of Forest Research 26:2134–2144.

McMahon, S. M., S. P. Harrison, W. S. Armbruster, P. J. Bartlein, C. M. Beale, M. E. Edwards, J. Kattge, G. Midgley, X. Morin, and I. C. Prentice. 2011. Improving assessment and modelling of climate change impacts on global terrestrial biodiversity. Trends in Ecology & Evolution 26:249–259.

Moore, J.-D., and R. Ouimet. 2006. Ten-year effect of dolomitic lime on the nutrition, crown vigor, and growth of sugar maple. Canadian Journal of Forest Research 36:1834–1841.

Moore, J.-D., R. Ouimet, R. P. Long, and P. A. Bukaveckas. 2014. Ecological benefits and risks arising from liming sugar maple dominated forests in northeastern North America. Environmental Reviews 23:66–77.

Moore, T., J. Trofymow, B. Taylor, C. Prescott, C. Camire, L. Duschene, J. Fyles, L. Kozak, M. Kranabetter, and I. Morrison. 1999. Litter decomposition rates in Canadian forests. Global Change Biology 5:75–82.

Morse, C. C., I. V. Yevdokimov, and T. H. DeLuca. 2000. In situ extraction of rhizosphere organic compounds from contrasting plant communities. Communications in Soil Science & Plant Analysis 31:725–742.

Moukoumi, J., R. E. Farrell, K. J. C. Rees, R. K. Hynes, and N. Bélanger. 2012. Intercropping *Caragana arborescens* with *Salix miyabeana* to satisfy nitrogen demand and maximize growth. BioEnergy Research 5:719–732.

Nezat, C. A., J. D. Blum, R. D. Yanai, and S. P. Hamburg. 2007. A sequential extraction to determine the distribution of apatite in granitoid soil mineral pools with application to weathering at the Hubbard Brook Experimental Forest, NH, USA. Applied Geochemistry 22:2406–2421.

Niinemets, Ü. 2010. Responses of forest trees to single and multiple environmental stresses from seedlings to mature plants: past stress history, stress interactions, tolerance and acclimation. Forest Ecology and Management 260:1623–1639.

Northup, R. R., Z. Yu, R. A. Dahlgren, and K. A. Vogt. 1995. Polyphenol control of nitrogen release from pine litter. Nature 377:1161–1167.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. O'Hara, G. L. Simpson, P. Solymos, M. Stevens, and H. Wagner. 2013. Community Ecology Package 'vegan'. R package version 2.0-10. https://cran.r-project.org/package=vegan

Oliet, J. A., J. Puértolas, R. Planelles, and D. F. Jacobs. 2013. Nutrient loading of forest tree seedlings to promote stress resistance and field performance: a Mediterranean perspective. New Forests 44:649–669.

Ouimet, R., P. A. Arp, S. A. Watmough, J. Aherne, and I. DeMerchant. 2006. Determination and mapping critical loads of acidity and exceedances for upland forest soils in Eastern Canada. Water, Air, and Soil Pollution 172:57–66.

Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42.

Penn, C. A., B. C. Wemple, and J. L. Campbell. 2012. Forest influences on snow accumulation and snowmelt at the Hubbard Brook Experimental Forest, New Hampshire, USA. Hydrological Processes 26:2524–2534.

Peres-Neto, P. R., P. Legendre, S. Dray, and D. Borcard. 2006. Variation partitioning of species data matrices: estimation and comparison of fractions. Ecology 87:2614–2625.

Pinheiro, J., D. Bates, S. DebRoy, and D. Sarkar. 2014. nlme: linear and nonlinear mixed effects models. R package version 3.1–117. https://cran.r-project.org/package=nlme

Quideau, S., O. Chadwick, R. Graham, and H. Wood. 1996. Base cation biogeochemistry and weathering under oak and pine: a controlled long-term experiment. Biogeochemistry 35:377–398.

Quirk, J., D. J. Beerling, S. A. Banwart, G. Kakonyi, M. E. Romero-Gonzalez, and J. R. Leake. 2012. Evolution of trees and mycorrhizal fungi intensifies silicate mineral weathering. Biology Letters 8:1006–1011.

R Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Rosenzweig, C., et al. 2008. Attributing physical and biological impacts to anthropogenic climate change. Nature 453:353–357.

Saucier, J., A. Robitaille, and P. Grondin. 2009. Cadre bioclimatique du Québec. Écologie forestière. Manuel de foresterie. Second edition. Ordre des ingénieurs forestiers du Québec: 186–205.

Schaberg, P. G., J. W. Tilley, G. J. Hawley, D. H. DeHayes, and S. W. Bailey. 2006. Associations of calcium and aluminum with the growth and health of sugar maple trees in Vermont. Forest Ecology and Management 223:159–169.

Soil Classification Working Group. 1998. The Canadian system of soil classification. Agriculture and Agri-Food Canada, Publication 1646. Revised third edition. NRC Research Press, Ottawa, Ontario, Canada.

St. Clair, S. B., W. E. Sharpe, and J. P. Lynch. 2008. Key interactions between nutrient limitation and climatic factors in temperate forests: a synthesis of the sugar maple literature. Canadian Journal of Forest Research 38:401–414.

Stenberg, P., S. Linder, H. Smolander, and H. Flower-Ellis. 1994. Performance of the LAI-2000 plant canopy analyzer in estimating leaf area index of some Scots pine stands. Tree Physiology 14:981–995.

Strobl, C., J. Malley, and G. Tutz. 2009. An introduction to recursive partitioning: rationale, application, and characteristics of classification and regression trees, bagging, and random forests. Psychological Methods 14:323.

Trofymow, J., T. Moore, B. Titus, C. Prescott, I. Morrison, M. Siltanen, S. Smith, J. Fyles, R. Wein, and C. Camiré. 2002. Rates of litter decomposition over 6 years in Canadian forests: influence of litter quality and climate. Canadian Journal of Forest Research 32: 789–804.

Van Breemen, N., R. Finlay, U. Lundström, A. G. Jongmans, R. Giesler, and M. Olsson. 2000. Mycorrhizal weathering: A true case of mineral plant nutrition? Biogeochemistry 49:53–67.

Wendel, G. W., and H. C. Smith. 1990. *Pinus strobus* L. Eastern white pine. Pages 476–488 *in* R. M. Burns and B. H. Honkala, editors. Silvics of North America: 1. Conifers. Agriculture handbook. USDA Forest Service, Washington, D.C., USA.

Whittaker, R. H. 1970. Communities and ecosystems. MacMillan, New York, New York, USA.

Wilson, J. B., and A. D. Agnew. 1992. Positive-feedback switches in plant communities. Advances in Ecological Research 23:263–336.

Wirth, C. 2005. Fire regime and tree diversity in boreal forests: implications for the carbon cycle. Pages 309–344 *in* M. Scherer-Lorenzen, C. Körner, and E. D. Schulze, editors. Forest diversity and function. Ecological studies (analysis and synthesis). Volume 176. Springer, Berlin, Germany.

Woodward, F. 1987. Stomatal numbers are sensitive to increases in CO_2 from preindustrial levels. Nature 327:617.

Yawney, H. W., and C. M. Carl Jr. 1968. Sugar maple seed research. Pages 115–123 *in* Proceedings, Twentieth Anniversary Nurserymen's Conference, September. USDA Forest Service, Northeastern Area State and Private Forestry, Upper Darby, Pennsylvania, USA.

Zhu, K., C. W. Woodall, and J. S. Clark. 2012. Failure to migrate: lack of tree range expansion in response to climate change. Global Change Biology 18: 1042–1052.

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2022/full